J. exp. Biol. ***182****, 1–10 (1993)*
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GEOMAGNETIC ORIENTATION OF LOGGERHEAD SEA TURTLES: EVIDENCE FOR AN INCLINATION COMPASS

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Accepted 10 May 1993

Summary

Recent experiments have demonstrated that hatchling loggerhead sea turtles can orient using the earth's magnetic field. To investigate the functional characteristics of the loggerhead magnetic compass, we tested the orientation of hatchlings tethered inside a circular arena surrounded by a coil system that could be used to reverse the vertical and horizontal components of the ambient field. Hatchlings tested in darkness in the earth's magnetic field were significantly oriented in an eastward direction. Inverting the vertical magnetic field component resulted in an approximate reversal of orientation direction, whereas reversing both the vertical and horizontal components together did not. The hatchlings failed to orient in a horizontal field of earth-strength intensity. These results provide evidence that the magnetic compass of loggerheads is an inclination (axial) compass, functionally similar to that of birds.

Introduction

Sea turtle hatchlings emerge from underground nests, scramble to the ocean and immediately begin swimming towards open water. Hatchling loggerhead sea turtles (*Caretta caretta* L.) from nests on the east coast of Florida quickly establish well-oriented offshore headings, presumably towards the Gulf Stream current (Salmon and Wyneken, 1987) and the North Atlantic gyre (Carr, 1986). Although the orientation cues guiding migration are not fully understood, field experiments indicate that turtles released offshore initially orient by swimming into approaching waves (Salmon and Lohmann, 1989). Recent laboratory experiments have also indicated that hatchling loggerheads possess a magnetic compass sense that may function during the offshore migration (Lohmann, 1991).

Although loggerhead hatchlings are capable of orienting to the earth's magnetic field, the functional characteristics of their magnetic compass have not been investigated.

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Key words: magnetic, magnetoreception, orientation, sea turtle, *Caretta caretta.*

Evidence has been reported for two functional types of magnetic compasses in animals. Birds appear to rely on an inclination (axial) compass that does not distinguish the polarity of field lines (i.e. north *versus* south); instead, the bird compass functionally defines 'poleward' as the direction along the earth's surface in which the angle formed between the total field vector and the gravity vector is smallest (Wiltschko and Wiltschko, 1972). For an animal with an inclination compass, inverting the vertical component of the ambient field has the same behavioral effect as reversing the horizontal component (Wiltschko and Wiltschko, 1988).

In contrast to inclination compasses, polar compasses determine north using the polarity of the horizontal field component; inverting the vertical component of the ambient field thus has no effect on orientation mediated by a polar magnetic compass. Because reversing the vertical component does not affect the orientation of magnetically sensitive sockeye salmon (Quinn *et al.* 1981) and African mole rats (Marhold *et al.* 1991), these animals may rely on polar compasses.

To determine whether loggerheads have a polar or an inclination compass, we studied the orientation of turtles swimming in darkness under four different magnetic field conditions. The data suggest that loggerheads possess an inclination compass functionally similar to that reported for European robins (Wiltschko and Wiltschko, 1972, 1988).

Materials and methods

Animals

Hatchling loggerheads were obtained from a nesting beach in Boca Raton, Palm Beach County, Florida, USA. Nests were checked daily for signs of recent hatching activity (i.e. depressions in the sand above nests) and excavated. Two or three hatchlings were removed, placed in styrofoam boxes and transported 4.0km to a laboratory at Florida Atlantic University. Hatchlings were maintained in darkness until approximately 19:00 h when tests began. Each hatchling was tested once within 24h of capture, then released.

Orientation tanks and data acquisition

Hatchlings were tethered in a nylon–lycra harness which did not restrict locomotor movement (Salmon and Wyneken, 1987). The harness was connected by a short (8.0cm) monofilament line to a lever arm which rotated freely in the horizontal plane. The arm was mounted on a post in the center of a 1.1m diameter plastic circular pool. The pool was filled with sea water to a depth of 15cm. Within the central post were photocells which translated angular position of the lever arm into electrical signals sent to a computer. Software was designed to record hatchling direction and swimming/resting activity at 10s intervals. Printouts summarized the orientation of each hatchling, including: (i) time spent in each of eight 45° sectors, and (ii) the sequence of a turtle's movements (i.e. the time a hatchling spent in a given sector before moving into an adjacent sector). These data formed the basis for criteria which separated random movement within the tank (circling) from periods of oriented swimming (see below).

Control of the ambient magnetic field

The pool was surrounded by two independent coil systems (Fig. 1). A Helmholtz coil, consisting of two square coils 1.5m on each side, was used to reverse the vertical component of the ambient field. A Rubens coil (Rubens, 1945), 1.6m on each side, was aligned with the north–south geomagnetic axis. It was used to reverse the horizontal component of the magnetic field. Each coil was connected to a separate d.c. power supply. Measurements of field intensity were made with a Schonstedt single-axis fluxgate magnetometer (model DM-2220).

The coil systems were used to produce four magnetic field conditions which varied in their horizontal and/or vertical components but not in total field strength. In the first (geomagnetic field) condition, the Rubens coil was used to enhance the ambient field in the laboratory slightly, thereby generating an earth-strength field which matched conditions outdoors (horizontal component of 0.028mT; vertical component of 0.039mT; total field strength of 0.048mT; inclination angle of 55˚). Field enhancement was necessary because steel beams in the walls and ceiling of the laboratory slightly diminished the total field strength inside the laboratory.

In the second field condition, the vertical component was reversed while the horizontal

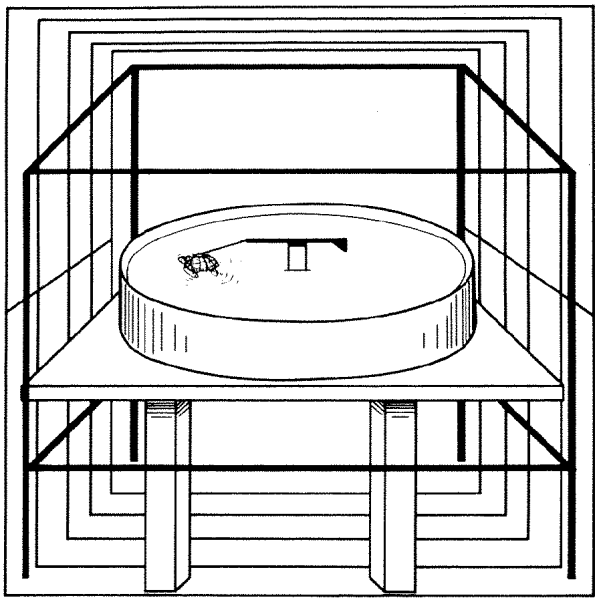

Fig. 1. The orientation apparatus. Hatchlings were tethered to a lever arm which rotated horizontally above a central post within a seawater-filled, circular pool. The pool was surrounded by a Rubens cube coil (thin lines) that could be used to reverse the direction of the horizontal component of the ambient field. In addition, a Helmholtz coil consisting of two square coils (one above the pool and one below) could be used to invert the vertical component of the field. The Helmholtz coil and its supporting stand are represented with thick lines. The Rubens coil and Helmholtz coil were each connected to a separate power supply. See text for further details.

component remained unchanged. In the third condition, both the vertical and horizontal components were reversed. To produce the fourth condition (a horizontal field), the vertical component of the earth's field was cancelled with an opposing field generated by the Helmholtz coil, while the horizontal field was enhanced (with the Rubens coil) to match the total intensity of the geomagnetic field outdoors.

Testing procedure

The orientation pool was located in a windowless, light-tight room. Experiments began at 19:00h. A turtle was harnessed and released in the pool with all of the room lights off except for a dim, frosted 15W bulb suspended in the east just above the water's edge. The light was provided for two reasons. First, since normal hatchlings swim towards light sources (Salmon and Wyneken, 1987), this response demonstrated that each turtle was behaviorally and physiologically competent. Those few hatchlings (<5%) that failed to hold a course towards the light were replaced with other turtles. Second, hatchlings which swim for about 1h towards a light continue to orient in that direction after the light is extinguished; while doing so, they use magnetic cues (Lohmann, 1991).

In our experiments, each hatchling was first exposed to the east light in an earth-strength (0.048mT) field for 1h. The light was then turned off and the turtle's orientation was monitored for the next 3h as it swam in darkness under one of the four magnetic treatment conditions.

Two hatchlings from one nest were tested each night under identical magnetic conditions. Treatments were changed every few days so that trials under each condition were conducted throughout the nesting season.

Swimming behavior of hatchlings

In darkness, tethered hatchlings manifest two distinct patterns of behavior, termed circling and oriented swimming (Lohmann, 1991). During circling, swimming results in gradual lateral clockwise or counterclockwise displacements so that turtles slowly move around the periphery of the arena, spending equal amounts of time swimming towards all directions. In contrast, hatchlings engaged in oriented swimming greatly reduce lateral movements and consistently maintain a course towards a specific direction. Such periods are usually short (3–12min) and are typically interspersed with longer periods of circling. An oriented swimming period (OSP) is defined as an interval of 3min or longer during which a hatchling remains in a single 90˚ sector of the arena (Lohmann, 1991).

Calculation of mean angle and statistics

Because circling turtles spend equal amounts of time in all parts of the arena and do not manifest directional preferences (Lohmann, 1991), analyses were based solely on directional preferences during oriented swimming periods. The analysis began at the point in the record when a hatchling had completed one circle of the pool during the dark period (within 1–5min after the light had been turned off). This allowed the hatchling to adjust to the dark condition and prevented the inclusion in the data of an oriented period resulting from a continuation of the response towards the formerly lighted sector.

A computer program analyzed the data and identified all oriented swimming periods

that occurred within 3h after the light had been turned off. Using standard procedures for circular statistics (Batschelet, 1981), the program then calculated a mean angle for each period based on all consecutive 10s readings which occurred while a hatchling remained in a single 90˚ sector. Thus, for example, the mean angle for a 3-min OSP was calculated from 19 readings (the orientation at the start of the period, plus six readings per minute for 3 min), whereas the mean angle for a 4-min OSP was based on 25 readings (the reading at time 0, plus six readings per minute for 4min).

On average, turtles had 8.42 OSPs (range 1–27) over the 3h dark period of data collection. In the final step of the analysis, the mean angles for all oriented swimming periods of a hatchling were used to calculate a final mean angle for that turtle. Thus, all data for each animal were ultimately reduced to a single angle representing the average direction towards which the hatchling swam during its periods of oriented swimming.

After experiments had been concluded, mean angles of all turtles in each of the four experimental groups were analyzed to determine (1) whether each group of hatchlings was significantly oriented (using the Rayleigh test); (2) whether the distributions in each of the four treatments differed significantly from one another (using the Watson test); and (3) whether the responses of the turtles were consistent with predictions of the inclination compass model proposed by Wiltschko and Wiltschko (1972).

Results

Turtles tested in the geomagnetic field were significantly oriented with a mean angle of 86˚ (Fig. 2A; N=16, P<0.05). Those tested in the field with a reversed vertical component (Fig. 2B) oriented in approximately the opposite direction (mean angle 296˚, N=46, P<0.01). Hatchlings tested in a field with both the vertical and horizontal components reversed (Fig. 2C) had an orientation similar to that in the earth's field (mean angle 117˚, N=16, P<0.05). Hatchlings tested in a horizontal earth-strength magnetic field (Fig. 2D) had an orientation statistically indistinguishable from random (N=16, P>0.20).

The distributions obtained in the geomagnetic field and in the field with the inverted vertical component were significantly different (Watson test, U^2=0.353, P<0.005). The distribution obtained when the vertical component was reversed also differed significantly from that obtained in the reversed vertical/reversed horizontal condition (U^2=0.364, P<0.002). Finally, the distributions obtained in the geomagnetic field and in the reversed vertical/horizontal condition were not significantly different (U^2=0.037, P<0.50).

Discussion

Evidence for a magnetic inclination compass in loggerheads

When tested in darkness in an earth-strength magnetic field, hatchling loggerheads oriented nonrandomly towards the east (Fig. 2A). These results are similar to those obtained by Lohmann (1991) working in a different location, in a different year and with a different coil system, orientation arena and data acquisition system. We have therefore

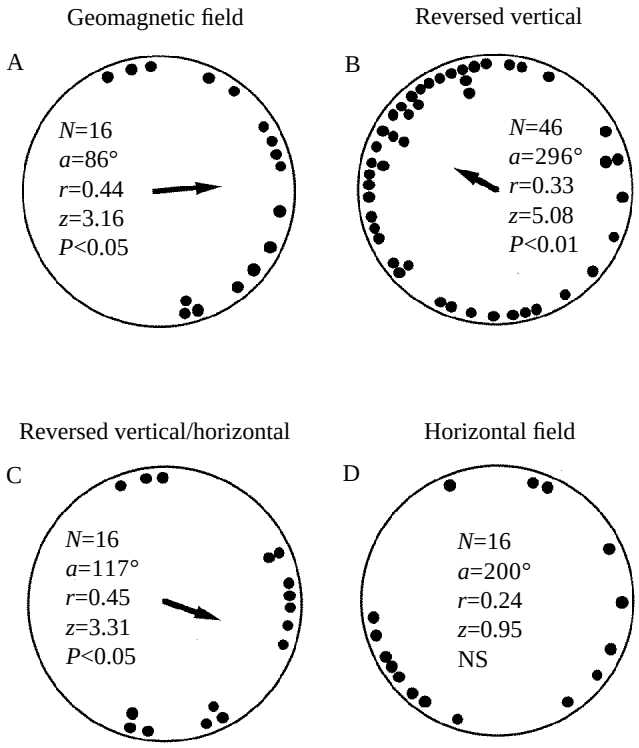

Fig. 2. Results of experiments under the four magnetic field conditions. Each data point represents the mean angle of orientation (*a*) for a single hatchling. Arrows show the mean angle of orientation for all turtles exposed to one field condition. Turtles tested under the geomagnetic field condition (A) were significantly oriented towards the east. In contrast, those tested in the field with the reversed horizontal component (B) were significantly oriented, but the mean angle of the group was shifted 150° relative to the geomagnetic controls. Hatchlings tested in the field with both the vertical and horizontal components reversed (C) had orientation similar to that of hatchlings tested under geomagnetic field conditions (A). Hatchlings exposed to a horizontal earth-strength magnetic field (D) had orientation statistically indistinguishable from random ($P>0.40$). Field intensity under each condition was identical (0.048mT). *N*, number turtles tested; NS, not significant.

replicated the finding that hatchling loggerheads are able to orient nonrandomly in darkness.

When the vertical component of the ambient magnetic field was reversed, the mean angle of orientation shifted by 150° (Fig. 2B). Thus, inverting the vertical component of the ambient magnetic field had the same qualitative effect as reversing the horizontal component of the field (Lohmann, 1991); each treatment resulted in an approximate reversal of orientation direction. These results are consistent with the predicted behavior of animals relying on magnetic inclination compasses (Wiltschko and Wiltschko, 1972, 1988).

The results obtained with loggerheads closely parallel those obtained for the European robin *Erithacus rubecula* (Wiltschko and Wiltschko, 1972). In both species, reversing

field polarity while leaving the inclination angle unchanged had no effect on orientation. In addition, inverting the vertical component had the same effect on orientation as reversing the horizontal component (Lohmann, 1991). Finally, both birds and turtles failed to orient in a horizontal earth-strength field (Fig. 2D). Although a polar compass (such as a standard mariner's compass) tracks the direction of the horizontal field component, an inclination compass is unable to distinguish between 'poleward' and 'equatorward' when field lines are parallel to the earth's surface (Wiltschko and Wiltschko, 1972). Thus, our results provide evidence that the loggerhead compass is based on inclination and is functionally similar to the bird magnetic compass.

Although the magnetic compasses of both birds and sea turtles appear to be based on field line inclination rather than on field polarity, evidence suggests this is not the case for all animals. For example, sockeye salmon (*Oncorhynchus nerka*) can orient to the earth's magnetic field (Quinn, 1980). Inverting the field vertical component does not cause a reversal of orientation in this species (Quinn *et al.* 1981). Similarly, the African mole rat (*Cryptomys hottentotus*) can orient using the earth's magnetic field (Burda *et al.* 1990), but inverting the vertical component has no apparent effect (Marhold *et al.* 1991). Thus, salmon and mole rats may have polar magnetic compasses with different functional characteristics from the compasses of birds and turtles.

The newt *Notophthalmus viridescens* appears to possess both an inclination compass and a polar compass. The inclination compass is used for short-distance movements towards shore, whereas a polar compass is used in long-distance homing (Phillips, 1986). It remains to be determined whether this apparent duality of compasses is based upon two independent magnetoreception systems or upon different neural processing of information from a single set of receptors.

Inclination compasses at the magnetic equator

At the magnetic equator, where field lines are parallel to the surface of the earth, an inclination compass will not provide directional information. Moreover, because an inclination compass distinguishes between 'poleward' and 'equatorward' rather than north and south, swimming 'poleward' in the two hemispheres leads in opposite directions. Whether loggerheads cross the magnetic equator is not known; relatively few loggerheads nest near the magnetic equator, although turtles are found in both hemispheres (Dodd, 1988).

Even if loggerheads do cross the magnetic equator, they may experience no difficulties in orientation. Recent studies suggest that migrating birds can use an inclination compass to initiate a course in one hemisphere and to maintain it after entering the other. Exposure to a horizontal earth-strength field simulating conditions at the magnetic equator results in a reversal of the response to inclination angle in some birds (Wiltschko and Wiltschko, 1992; Beason, 1992). Such a response would be appropriate for a migrant which moves from the northern into the southern hemisphere, then later makes a return migration.

Multiple cues in sea turtle orientation

Our results and previous experiments (Lohmann, 1991) have demonstrated that in the laboratory, hatchling loggerheads can derive directional information from the earth's

magnetic field. Under natural conditions, this ability may be augmented or supplanted during migration by other sensory cues. The use of multiple cues has been repeatedly demonstrated (e.g. birds possess magnetic, sun and star compasses; Able, 1991).

Like birds, sea turtles probably rely on multiple cues while migrating. Experiments have demonstrated, for example, that hatchling sea turtles released near shore initially swim into approaching waves, even when doing so leads them back towards land (Salmon and Lohmann, 1989; Lohmann and Lohmann, 1992). In deeper water far from shore, hatchlings may rely on a combination of waves, magnetic cues and as yet unidentified directional guideposts (Lohmann, 1992). Thus, the earth's magnetic field is probably only one of several cues used by hatchlings in the course of their offshore migration.

The present study raises many additional questions regarding the function of the magnetic compass in sea turtles. Further research investigating the sensitivity of the compass, ontogenetic changes in orientation, the mechanism of magnetic field detection and the transfer of directional information between sensory systems is needed to address these issues.

We thank the Gumbo Limbo Nature Center in Boca Raton, Florida, for providing access to sea turtle nests and hatchlings. Earlier drafts were improved by comments provided by C. Lohmann, P. Lutz, A. Marsh and J. Wyneken. J. Fairchild, A. Prochaska and J. Vanderventer designed and constructed the orientation system and software used in our experiments. This research was completed by P. Light to partially fulfill the requirements for a Master of Science degree at Florida Atlantic University. The study was conducted under Florida DNR special permit TP 073 and was supported by grants from the NSF (BNS-87–07173; IBN-9120338).

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